

SELECTION OF MICROHABITAT BY THE INTRODUCED MEDITERRANEAN GECKO, *HEMIDACTYLUS TURCICUS*: INFLUENCE OF AMBIENT LIGHT AND DISTANCE TO REFUGE

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ABSTRACT—The Mediterranean gecko (*Hemidactylus turcicus*) is an introduced nocturnal lizard that often can be seen on and around buildings in the southern United States and in its native Old World range. However, little is known about the factors that determine its selection of microhabitat, except that it does not actively thermoregulate. For example, geckos may forage near lights due to presence of higher concentrations of flying insects or they may select darker sites near refugia to avoid predators. This study investigates the influence of ambient light level (irradiance) and distance to a refuge on selection of microhabitat. During their normal activity period, 54 geckos were hand captured. Snout-vent length, mass, sex, irradiance, and distance to the nearest refuge (crack, crevice, or hole) were determined for each lizard at the time and place of capture. Juvenile geckos tended to be in areas with higher irradiance and farther from refugia than adults. All adults generally selected sites closer to refugia. Adult male and female geckos did not differ significantly in selection of microsites. Thus, we suggest that adult lizards, especially territorial males, exclude juveniles from sites closer to refugia, which are typically of lower irradiance.

RESUMEN—El gecko Mediterráneo (*Hemidactylus turcicus*) es una lagartija nocturna introducida en los Estados Unidos que se encuentra en y alrededor de edificios en el sur de los Estados Unidos y en su territorio nativo del viejo mundo. Sin embargo, los factores que determinan su preferencia de microhabitat son en gran parte desconocidos, excepto por su inhabilidad de termoregulacion. Por ejemplo, geckos podrían elegir cazar cerca de lugares iluminados debido a la presencia de insectos; podrían escoger sitios oscurecidos y cercanos a sus refugios para evitar depredadores; podrían elegir microhabitats con una combinación de estas dos alternativas; o quizás preferirían un microhabitat con otra características de mayor importancia. Este estudio investiga como el nivel de luz ambiente ("irradiance") y distancia a un refugio influyen la selección del microhabitat. Cien y cuatro (54) geckos fueron capturados a mano durante períodos de actividad normal. La longitud del hocico-ventre, la masa, el sexo, nivel de luz ambiente, y distancia al refugio más cercano (hoyo o grieta) fueron medidos al momento y lugar de captura de cada gecko. Geckos juveniles suelen encontrarse en areas de alto nivel de luz ambiente y mas lejano de refugio. Geckos adultos en general prefirieron sitios mas cercanos a refugio. Las hembras prefirieron sitios oscuros mientras que los machos fueron encontrados en microhabitats con alta irradiación, pero, geckos machos escogieron sitios más cercanos al refugio comparado a las hembras. Por lo tanto sugerimos que los geckos adultos, especialmente machos territoriales, excluyen a geckos juveniles de sitios más cercanos a refugios los cuales típicamente son de bajos niveles de luz ambiente.

Selection of microhabitat is of paramount importance to animals because of the high costs associated with poor choices (Huey, 1991; Webb et al., 2004). For example, if an animal chooses a thermally inappropriate microhabitat, then it will face reduced physiological performance, which would reduce its overall fitness (Huey, 1991). Because the struggle to maximize fitness is a driving force for all organisms, animals should select microhabitats that allow them to

attain the greatest fitness possible (Fretwell and Lucas, 1970; Rosenzweig, 1981). Many factors, including risk of predation, access to food, and interspecific and intraspecific competition, can influence the fitness of an animal, and consequently, selection of microhabitat by that animal (Anderson, 2007).

Much research on selection of microhabitat in lizards has been conducted on diurnal species with an emphasis on thermal properties (Heat-

wole, 1977; Hertz et al., 1994; Downes, 2001; Webb et al., 2004). However, environmental conditions at night limits the effectiveness of thermoregulation because thermal inputs (i.e., solar radiation) are not available (Hitchcock and McBrayer, 2006). Hitchcock and McBrayer (2006) reported that the Mediterranean gecko, *Hemidactylus turcicus*, an introduced, Old World, nocturnal, gekkonid lizard (Connant and Collins, 1998), does not actively thermoregulate during its normal activity period because there is a narrow range of available microclimates. Thus, temperature is not likely a key variable affecting selection of microhabitat in this nocturnal species.

Heatwole (1977) suggested that studies of selection of microhabitat in reptiles should include other characteristics (e.g., distance to refugia) as indicators of quality and therefore choice of microhabitat. While active, *H. turcicus*, and other scansorial lizards commonly avoid predation by using known escape routes to refugia (Selcer, 1986; Braña, 2003). Because Mediterranean geckos are thermoconformers and are active at temperatures below their measured optimum temperatures for locomotion (Huey et al., 1989; Autumn et al., 1997; Hitchcock and McBrayer, 2006), they provide an opportunity to investigate other characteristics of quality of microhabitat in the absence of confounding affects of temperature.

Within the microhabitat of an animal, the microsite (=nanohabitat) is the specific area, often no larger than the size of an animal, where an animal is found and specific behavioral acts occur (Anderson, 2007). Selection of optimal characteristics at the microsite scale in selection of microhabitat potentially has the greatest consequences for obtaining optimal physiological states (e.g., thermoregulation, foraging, and digestion) and survival (e.g., inconspicuousness, fleeing a predator). For instance, distance to refuge could be an important aspect in selection of microsite for avoidance of predators. Braña (2003) suggested that being close to a refuge allows lizards to reach safety during an attack without attaining maximum running speeds, thus conserving energy. Therefore, distance to refugia could potentially be important to selection of microsite, and for diurnal lizards, likely also influences selection of optimal basking sites (Braña, 2003). In a nocturnal, thermoconforming lizard like *H. turcicus*, avoidance of risk likely

plays a crucial role in an assessment of overall quality of microhabitat because environmental thermal variation is negligible (Hitchcock and McBrayer, 2006). Furthermore, Howard et al. (2001) observed that three species of geckos (including one congener, *H. mabouia*) on the Lesser Antilles island of Anguilla tended to occur on structurally complex buildings (i.e., buildings with many crevices, angles, and much associated debris) and speculated that this pattern was due to an increased availability of refuges on such buildings.

Another potentially important factor of selection of microsite is irradiance (ambient light intensity). Several studies (Selcer, 1986; Saenz, 1992; Capula and Luiselli, 1994; Connant and Collins, 1998) have observed anecdotally that *H. turcicus* tends to be seen around light fixtures on outer walls of buildings. There is some evidence that some diurnal lizards use light as a proximate cue to quality of microsite with respect to thermal suitability and maximization of the efficiency of visual sexual displays (Hertz et al., 1994; Leal and Fleishman, 2002). Presence of a gecko near a light source has been assumed to be related to foraging (e.g., increasing chances of encountering flying insects). Because *H. turcicus* does consume some flying insects (Saenz, 1996), and is an ambush predator that relies heavily on vision (Rose and Barbour, 1968), increased ambient light levels could certainly aid foraging success in this species. However, *H. turcicus* also has been demonstrated to use hearing to prey upon crickets (Sakaluk and Belwood, 1984). In a portion of its native range, Egypt, *H. turcicus* is completely nocturnal (i.e., active most often in complete darkness; Ibrahim, in press). Moreover, *H. turcicus* readily captures prey that usually is not associated with sources of light and do not make sounds like crickets (e.g., Aranea and Isopoda; Saenz, 1992). Thus, the observation that geckos often are seen around lights may be an artifact of the reliance of human observers on lights to see them or they may be using them to increase foraging efficiency. These conflicting findings led us to evaluate the relationship between irradiance and selection of microsite (i.e., selection of microhabitat).

Interestingly, our study population of *H. turcicus* exhibits dietary niche partitioning in size and type of prey between adult males and females, as well as between adults and juveniles (Saenz, 1992, 1996). Saenz (1996) speculated

that reduced dietary overlap prevents intraspecific competition, but because territories of adult *H. turcicus* do not overlap (Klawinski, 1991), the reduced overlap in diet is due to differences in selection of microsite rather than differences in selection of prey. Because irradiance and distance to refugia have been used by other species of lizards as cues to quality of microhabitat (Hertz et al., 1994; Braña, 2003), it seems likely that these factors influence selection of microsite differently among adults and juveniles in *H. turcicus*.

We hypothesized that Mediterranean geckos of different body sizes and in different reproductive groups (i.e., juveniles, adult males, and adult females) would occur in microsites with different ambient light intensities (irradiance) and distances to refugia. Because distance to refuge may be a key factor in selection of microsite in scansorial lizards (Braña, 2003) and territories of adult *H. turcicus* seldom overlap (Klawinski, 1991), we hypothesized that older, more dominant (=larger) geckos would exclude younger, subordinate (=smaller) individuals and, thus, occur closer to refugia than smaller geckos. Additionally, microsites with higher irradiance could yield high foraging profits due to greater abundance of flying insects around them (Saenz, 1996). Consequently, individuals may risk moving into the open to forage rather than remain close to the safety of darkness. Thus, we hypothesize that older, more dominant (=larger) individuals will exclude younger subordinate (=smaller) individuals from brighter microsites. If irradiance and distance to refugia are important to *H. turcicus* in its selection of usable microhabitats, then significant differences in use of microsites should exist across a range of body sizes and reproductive groups (i.e., between juveniles and adults, as well as between adult males and females).

METHODS—This study was conducted on the Stephen F. Austin State University campus in Nacogdoches, Nacogdoches Co., Texas, 18 August–15 September 2004. The study site, the Shelton Gym Complex (94°38'50W, 31°37'10N), has a sizeable population of Mediterranean geckos and has been studied numerous times (Klawinski, 1991; Saenz, 1996; Hitchcock and McBrayer, 2006). This site contains ample refugia in the form of rain gutters, drain pipes, masonry expansion gaps, and low vegetation along the base of the walls. Globe-shaped street lamps and building lights provided a wide variety of light conditions. Three different walls of the Shelton Gym Complex, each with

differing amounts of light and access to refugia, were sampled. Data collection occurred during peak hours of activity for this species, which is immediately after complete darkness until about midnight (2100–2400 h; Rose and Barbour, 1968; Ibrahim, in press).

Individuals were captured by hand and their original position was marked with masking tape. Distance to any refuge (i.e., crack, crevice, or hole large enough to accommodate the size of the captured gecko) was measured from this initial sighting point. Also, at the initial sighting point, irradiance levels were measured in lux (lumens/m²) using an Extech 401235 digital light meter (Extech Instruments, Waltham, Massachusetts) held flat against the wall with the cosine correction dome (sensor) facing outward. Sex of adult individuals was determined by checking for presence of pre-anal pores and categorized into one of three reproductive groups (juvenile, adult male, or adult female). Sexually mature adults (males and females) were defined as individuals >44 mm snout–vent length (Selcer, 1986). Smaller individuals were categorized as juveniles (sexes not separated). Once snout–vent length was recorded, lizards were marked with non-toxic paint to prevent including recaptured individuals in statistical analyses. All geckos were released at their initial sighting point.

Raw data for ambient irradiance varied from 0 to 23.8 lux and was not normally distributed. Raw data for distance to refugia varied from 0 to 217 cm away, and also was not normally distributed. Data for each variable was centered by adding one to the raw values and then Log₁₀ transformed to achieve a normal distribution. The centered, transformed data were used in all statistical analyses. Analysis of variance (ANOVA) with Tukey-Kramer post-hoc tests were used to determine if there were significant differences among reproductive groups (juveniles, adult males, or adult females) in irradiance and distance to refugia among microsites. Because the groups of adult males, females, and juveniles largely reflect variation in body size, regression analysis was used to quantify the relationship between body size (snout–vent length) and distance to a refuge, as well as between body size and irradiance. Statistical analyses were conducted using NCSS 2004 statistical software.

RESULTS—A total of 54 individuals was captured. Of these, 20 were females, 17 were males, and 14 were juveniles (snout–vent length <44 mm). Size distribution of adults and juveniles showed that these age classes were separated by a gap of 9 mm in snout–vent length. This small gap in distribution of body size likely is due to periodicity of reproduction in this temperate climate, coupled with our sampling period (late summer). Adult females were similar in size to adult males in snout–vent length (Table 1). As expected, juveniles were considerably smaller than adults (Table 1).

Females occurred in the darkest microsites far from refugia (Table 1, Fig. 1). Juveniles were in

TABLE 1.—Variation in snout–vent length, distance to refugia, and irradiance in selection of microhabitat by *Hemidactylus turcicus* (mean \pm 1 SE).

Reproductive group	Snout–vent length (mm)	Distance to refugia (cm)	Irradiance (lux)
Male ($n = 14$)	53.00 \pm 0.93	22.22 \pm 10.56	4.19 \pm 2.31
Female ($n = 18$)	54.28 \pm 0.81	50.04 \pm 15.33	1.05 \pm 0.34
Juvenile ($n = 22$)	29.95 \pm 0.84	85.13 \pm 14.10	4.92 \pm 1.42
Groups combined ($n = 54$)	44.08 \pm 1.68	57.12 \pm 8.75	3.44 \pm 0.86

the brightest sites farthest from refugia (Table 1, Fig. 1). Males occurred in bright sites, although they exhibited a great deal of variability, and were closest to refugia (Table 1, Fig. 1).

Analyses of variation of both irradiance and distance to refugia showed significant differences among reproductive groups (Table 2). Tukey–Kramer post-hoc tests confirmed that there was a significant difference between females and juveniles in irradiance levels of microsites (Fig. 1). Adult males, however, showed no significant difference to either juveniles or adult females in irradiance at their microsites (Fig. 1). Tukey–Kramer post-hoc tests for distance to refugia confirmed that juveniles selected microsites that were farther from refugia compared to adults, but that adult males and females did not differ from one another in their proximity to a refuge (Table 1, Fig. 1).

Body size (snout–vent length) and irradiance had a significant inverse relationship ($b = 1.908$, $m = -0.917$; $T = -2.110$, $P = 0.032$) as did body size and distance to refugia ($b = 5.791$, $m = -2.720$; $T = -3.906$, $P < 0.001$). However, the strength of these relationships was generally low (irradiance, $R^2 = 0.09$; distance, $R^2 = 0.23$; Fig. 2).

DISCUSSION—This study shows that irradiance and distance to refugia are related to selection of microsite by *H. turcicus* and that these differences are largely between juveniles and adults. Large, adult geckos tend to occur in darker sites closer to refugia, whereas smaller, juvenile, geckos often were in brighter sites farther from refugia (Fig. 2). While there are many potential explanations for this pattern, the exclusion of smaller juveniles by larger adults from microsites that may be “preferred” seems the most likely explanation (Fretwell and Lucas, 1970; Anderson, 2007). Hitchcock and McBrayer (2006) noted that juvenile *H. turcicus* from this same locality selected microhabitats with smaller ranges in temperature than adults when pre-

sented with a wide range of microclimates in controlled experiments. These authors suggested that this difference may be due to juveniles trying to avoid conflict with adults that have set up territories in sites that are better in terms of their foraging opportunities or access to refugia. However, it also is possible that juveniles may just be naive in their choice of microsite, which could explain their high rates of mortality (Selcer, 1986). The finding that juveniles occur in brighter, more exposed areas, although they eat more arthropod prey associated with darker vegetated areas near the ground (e.g., homopterans and araneans; Saenz, 1992), seems more suggestive that they are being excluded from microsites that are selected for foraging or access to refugia.

The lack of significant differences between adult males and females in either irradiance or distance to refugia suggests that males and females in this species do not actively select different habitats, which is contrary to the suggestion of Saenz (1996). Differences in selection of microsite could be masked by the high variation in males with respect to irradiance (Table 1), or the timing of the sample period (mid-August to mid-September). The reproductive season of *H. turcicus* ends in early August (Rose and Barbour, 1968) and the post-reproductive season may lead to a shift in behavior. For instance, there may no longer be any need for partitioning of diet as found by Saenz (1996), or maintenance of territory and, thus, males and females begin competing for the same food sources in the most optimal microsites (dark places with lots of places to hide).

Gomez-Zlatar (2006) quantified selection of microhabitat by *H. turcicus* using categorical data (e.g., building surface material, vegetative cover, irradiance) and detected no significant pattern. Gomez-Zlatar (2006) provided several hypotheses to explain her results, including inadequate samples and irrelevance of the tested variables.

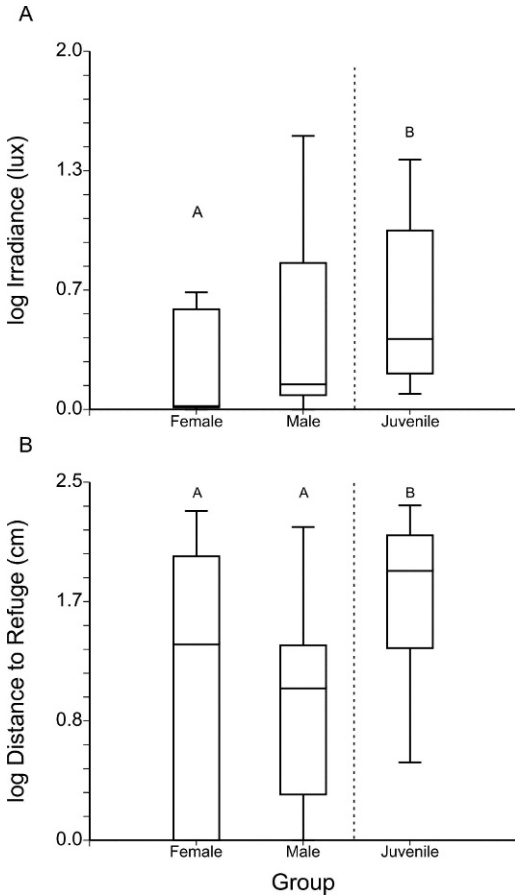


FIG. 1.—Box plot of microhabitat irradiance for adult males, adult females, and juveniles. Sex of geckos <44 mm snout-vent length was not determined, and they were categorized as juveniles. The dotted line separates reproductive groups. Tukey-Kramer multiple comparison tests indicated significant differences between: a) females and juveniles, but males were not different from either females or juveniles; b) juveniles and both males and females, but males and females were not different from each other.

She ultimately suggested that the extreme behavioral plasticity of *H. turcicus* allowed it to thrive in many different microhabitats and environmental situations. Considering the efficiency of *H. turcicus* as a colonizer (Selcer, 1986) and the low predictive power of both irradiance and distance to refugia in the present study, the suggestion by Gomez-Zlatar (2006) about the behavioral plasticity of this species has considerable merit.

The studies that have revealed most about selection of microsites (or microhabitats) by *H.*

turcicus have been investigations of foraging patterns (Rose and Barbour, 1968; Saenz, 1992, 1996; Klawinski et al., 1994). While it has been suggested that *H. turcicus* occurs around artificial lights because it is preying heavily upon flying insects, the diet of *H. turcicus* contains a high proportion of terrestrial arthropods that occur under rocks or in vegetation (e.g., isopods and spiders; Saenz, 1996). Thus, the generalist diet of *H. turcicus* (Rose and Barbour, 1968; Saenz, 1996) may also affect the wide range of microsites that this species occupies. Therefore, the tendency of *H. turcicus* to occur around lights may not be because the lizards are cueing on irradiance as an indicator of quality of foraging site, but perhaps, because density of prey around light fixtures is high and they offer access to refugia (e.g., behind the fixture itself). Darker areas, such as behind trash cans and in vegetative cover, which were both productive sites for capturing geckos, could offer the same characteristics of selected microsites. Thus, irradiance may only have an effect on choice of microsite because it is associated with some other more important characteristic of microsite (i.e., irradiance is a source of ecological noise). Experimental studies that manipulate abundance of prey, irradiance, and access to refugia will help tease these issues apart.

The greater amount of variation in selection of microsite accounted for by distance to refugia may reflect a greater importance of this variable to *H. turcicus*, as has been proposed by other researchers for other scansorial species (Braña, 2003). Due to the territorial nature of *H. turcicus* (Rose and Barbour, 1968; Selcer, 1986; Klawinski, 1991), one may expect large lizards to exclude smaller individuals from potentially valuable microsites. The predictive power of distance to refugia was low ($R^2 = 0.23$), but this value may be low due to sampling bias. A refuge was defined as rocks, cracks, holes, and other building structures, but the definition did not include vegetative cover. For example, plants growing along the base of the wall were excluded because many of the geckos that were captured were seen first within this vegetative cover and then fled to crevices in the wall. Also, not all of the walls had vegetative cover along their base. Perhaps, a wider definition of refugia that includes low vegetation near the ground would result in a stronger relationship (R^2) between distance to a refuge and choice of microsite.

TABLE 2—Results of analysis of variance showing differences in irradiance and in the distance to refugia among three reproductive groups of *Hemidactylus turcicus* (adult males, adult females, and juveniles). Results of post-hoc tests are shown in Fig. 1.

Variable	df	Sum of squares	Means square	F	P
Irradiance					
Sex	2	1.137	0.568	3.7	0.0315
Error	51	7.826	0.153		
Total	53	8.963			
Distance to refugia					
Sex	2	6.117	3.058	6.65	0.00271
Error	51	23.455	0.46		
Total	53	29.571			

Furthermore, this particular microsite (behind vegetation, but near light) likely offers the best of both worlds, crypsis due to shadows created by vegetation, yet also higher light levels filtering through the vegetation, which would benefit their ambush-foraging behavior.

While this study determined that distance to refugia and levels of irradiance differed among certain reproductive groups, the low amount of variation explained by these characteristics suggests that there are other factors or (more likely) complex interactions among many factors that affect microsite selection by *H. turcicus*. One likely scenario indicated by the findings of Saenz (1996), Gomez-Zlatar (2006), and this study is that abundance of prey attracts geckos to a site, which then forage as close to a refuge as possible, in the darkest site possible. Further studies with larger samples may use multivariate statistical techniques to explore this hypothesis.

Irradiance and distance to refugia are two elements of a potentially important and complex suite of characteristics of microhabitat that allows nocturnal lizards like *H. turcicus* to avoid predators in an energetically conservative manner, while also allowing them to operate at lower than optimal body temperatures (Huey, 1989; Autumn et al., 1997; Weinstein and Full, 1999; Braña, 2003; Hitchcock and McBrayer, 2006). Both characteristics examined in this study may contribute to avoidance of predators, in that they prevent an attack from occurring or allow a more efficient use of energy during an escape (e.g., a slower escape; Braña, 2003). However, other characteristics of the ecology of an animal may

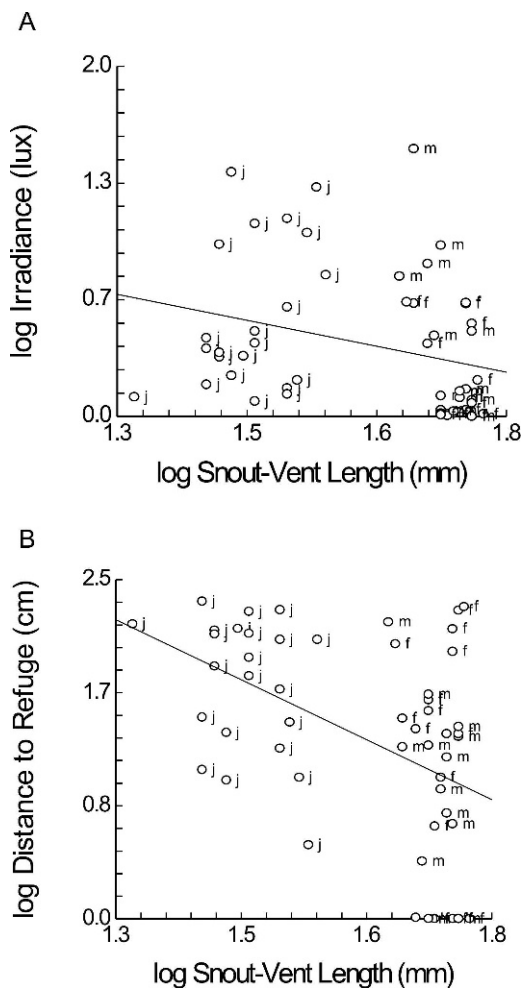


FIG. 2—Linear regressions showing inverse relationships between (a) microhabitat irradiance and snout-vent length ($n = 54$) and (b) distance to the nearest refugia from a microsite and snout-vent length ($n = 54$).

interact with either irradiance or distance to refugia reducing the importance if these two characteristics in broader selection of microhabitat. For example, the cryptic coloration exhibited by *H. turcicus* (Selcer, 1986) may reduce the importance of low irradiance in preventing an attack, subsequently reducing the importance of irradiance to quality of microsite. While the low amount of variation explained by irradiance suggests reduced importance of this characteristic to *H. turcicus*, irradiance may be of increased importance in other less-cryptically colored, nocturnal lizards. The ability to effectively avoid

encounters with predators could be highly beneficial to nocturnal lizards on an energetic basis (Braña, 1993, 2003). *Podarcis muralis*, a diurnal lizard, exhibits a direct, positive relationship between distance to refugia and the distance that a predator is allowed to approach (Braña, 1993). Thus, interactions between morphology (cryptic coloration) and behavior (selection of microhabitats and microsites) may play a key role in spacing and energetics of nocturnal lizards. Choice of microsite may also have some evolutionary impacts as well. For example, species of lizards that do not have as far to flee, may also circumvent pressures that select for morphologies that enhance running speed, such as long hind limbs (Pianka and Pianka, 1976).

The present study has identified distance to refugia as a component in selection of microsite by *H. turcicus*. Our findings suggest that body size (or age or social status) plays an important role in selection of microsite in this nocturnal species. Furthermore, our findings suggest that irradiance may be a source “noise” in that it has a limited role in selection of microsite, but we cannot rule out that it may be functionally linked to other variables (e.g., ambush foraging from a dark site near a refuge). Similar patterns are likely in other nocturnal species. Observational, deductive studies like this one and others (e.g., Howard et al., 2001; Gomez-Zlatar et al., 2006) are important to reveal which characteristics may be biologically relevant in larger models of selection of microsite and microhabitat and which characteristics may be misleading.

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